THE ANATOMY OF THE ADULT QUEEN AND WORKERS OF THE ARMY ANTS *ECITON BURCHELLI* WESTWOOD AND *ECITON HAMATUM* FABRICUS

Roy M. Whelden

[Continued]

THE REPRODUCTIVE SYSTEM

The reproductive system of *Eciton* is of interest, because of the queen's capacity for mass production of eggs, and also because of the significance the regular broods have for cyclic functions in the colonies (Schneirla, 1938, 1944, et seq.)

It is relevant to mention the regular variation in colony function and the condition of the colony queen as reported by Schneirla (1938, 1949, 1957) of *Eciton* under natural conditions. Schneirla's extensive studies have shown that the activities of both *Eciton hamatum* and *burchelli* present "a striking regularity in all of their principal colony operations, clearly related in its evolutionary background to the physical conditions of surface life. . . . Colony functions in these two species . . . center around two well-marked repetitive activity phases. . . . One of these is the nomadic phase, a period averaging 17 days in *E. hamatum* and 13 days in *burchelli* colonies; during this phase, the colony carries on extensive daily raids, followed by an emigration at the day's end. The other is the statary phase, a period of relative quiescence, during which raids are much smaller or occasionally absent, and the colony stationary in some sheltered place. The statary phase averages about 20 days in *E. hamatum* and 21 days in *burchelli.* During the nomadic phase, the brood comprises developing larvae, while in the statary phase, pupal development occurs, and also, during the last half, egg-laying and larval development of a new brood." In scores of colonies of *Eciton hamatum* and *burchelli,* and in numerous colonies of other species of this genus, the queens were always found contracted in the nomadic phase, entering physogastry near the end of this phase, progressing to maximal physogastry during the first week of the statary phase, and delivering the eggs of a new brood during the intermediate part of the statary phase (Schneirla, 1947).

Beginning at the posterior entrance and proceeding forward, the genital entrance may be observed as a long shallow space, bounded below by a thick membrane extending from the sclerotized wall of the 5th gastric segment to its anterior margin. Here it turns abruptly upward to form the bursa copulatrix a transversely elongate pouch, with a thick wall characterized by many unequal deep irregular folds, extending from one side of the pouch to the other. On the posterior-dorsal side, this wall joins the thin walls of the greatly modified 6th and 7th gastric segments lying alongside and above the sting. The size of this depends upon the extent of the folding of the walls, which sometimes leaves scarcely any free space within. In other individuals, the cavity is of some size and usually empty. No sperm mass was found therein but there were a few eggs in each of two queens, near the end of an egg-laying period. One queen taken in coitus (1946 H–L,—Schneirla, 1949) showed scarcely any folding of the pouch wall. This pouch is merely an adaptation to receive the posterior end of the large abdomen of the male; and has no other function. The surface of the ventral wall of the genital entrance is armed with many transverse rows of coarse spines from 10–50 μ long (Fig. 9, L, M). On the membrane forming the dorsal surface, spines are limited to small areas, mostly near the anterior part of this surface. There the spines, in transverse rows like those of the ventral surface, are smaller, slender, and with finely pointed apices. No spines occur on any part of the walls of the pocket.

The only opening into the genital entrance (except the large mouth of the bursa) is the vagina in the center of the anterior wall of the genital entrance. The vaginal opening is large and transversely elongate, the margins normally rather closely adpressed, except during the prolonged period of laying when the opening becomes enlarged and nearly circular.

The vagina is a thick-walled organ of variable dimensions. In some individuals, it is long, and of small diameter; in others, it is short but greater in diameter. These dimensions are not always correlated with the periodic changes in the reproductive system. For example, of two laying queens in fully physogastric condition, one has the diameter large with the vagina long and narrow; the other has the diameter small with the vagina scarcely half as long. In both queens a row of several eggs occurs in the lumen of the vagina.

The wall of the vagina is thick and has four distinct layers. The innermost is a thick homogeneous membrane, bearing slender, flexible setae on its inner surface. Surrounding this intima, is a layer of long uninucleate columnar cells comparable to the elongate hypodermal cells noted earlier. Outside this layer, are two layers of muscle fibres; the inner, of longitudinal fibres, is thin; the outer, of circular fibres, thicker. Enclosing these tissues, is a thin, scarcely discernable membrane. Near the end of an egg-laying period, eggs may be seen in the lumen of the vagina, sometimes only one or two, occasionally as many as six.

Anteriorly, the vagina joins the median oviduct. Usually, the union forms a straight tube with no distinction at the point of union; but individuals are found in which a sharp bend or even a S-shaped curve occurs where the oviduct joins the vagina.

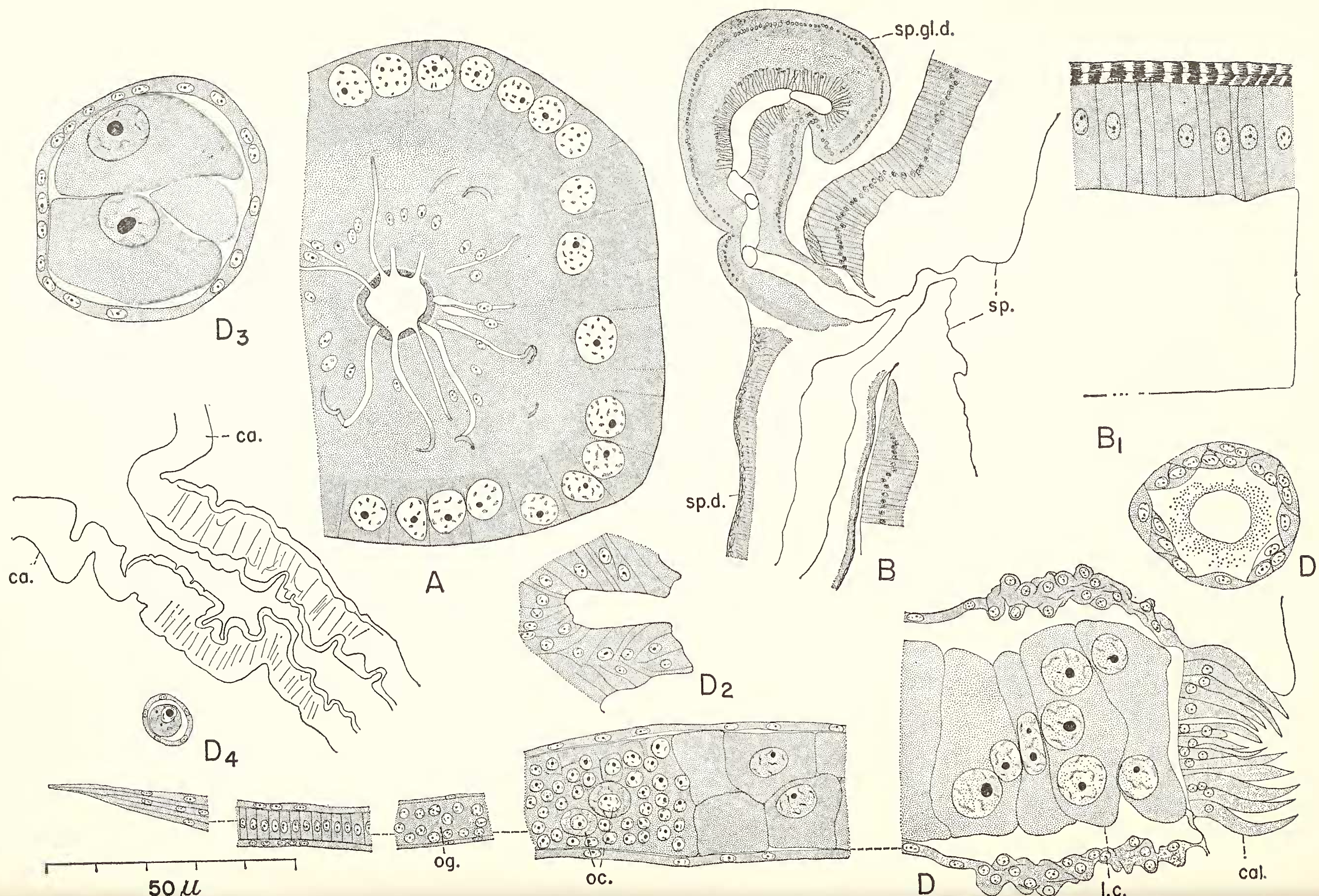
The median oviduct and the paired oviducts extending upwards from the anterior end of the median oviduct are similar in structure, being formed of three distinct layers. In contracted queens, the two inner layers are forced into deep closely adpressed folds, the entire wall measuring 50–65 μ in thickness (Fig. 12, E). The innermost layer is a membrane having an average thickness of 1–3 μ. In *hamatum* queens, on the inner surface of this membrane, towards the lumen, a few irregularly spaced acute spines about 2 μ long (Fig. 12, I) occur. These spines, directed posteriorly, do not seem to be pressed against the surface of the membrane on which they occur. In all contracted queens, the lumen of the oviduct is practically eliminated, so compactly is the wall adpressed. The greater part of the wall of the oviduct is formed of a layer of elongate cells having ellipsoidal nuclei, 4–6 μ long and 1.4–3 μ in maximum diameter. In contracted queens, they appear as radiating groups in each of the large folds of the wall (Fig. 12, I) : in physogastric queens, the wall becomes progressively thinner as swelling of the gaster progresses and the longitudinal muscles gradually become a sparse layer of fibres. The irregularly radiate cells of the middle layer are gradually pressed out until they are encircling muscle fibres; a few cells having nuclei much larger than the others occurring here (Fig. 12, G). The inner membrane becomes thin with the minute spines then lying closer to its surface. In *burchelli* queens, these spines become slightly thickened areas in an otherwise smooth wall. In contracted queens and those in early physogastry, the lumen of the oviducts is empty. As physogastry advances, eggs move first into the paired oviducts, and then to the median oviduct until the common oviduct at maximum physogastry may contain 10–24 mature eggs, and each of the paired oviducts 30–60 eggs. These eggs invariably have their long axis parallel to the long axis of the duct containing them. During this period, the outer longitudinal muscle fibres become widely and irregularly separated and the inner layer of muscle fibres clearly show their striated nature except in the region in which nuclei occur (Fig. 12, F, G, H). This inner muscle layer now has the fibres more irregularly separated. The occasional large nuclei still present are separated from the muscle tissues, and slightly flattened.

At the end of physogastry, the oviducts quickly shrink to their narrow state (Fig. 10, C).

At its upper end, each oviduct flares out into a large fusiform chamber, the calyx of the ovary; though the name does not seem apt in *Eciton*. The wall of this chamber may be separated into two areas of different structures most clearly seen in callow queens. One of these areas comprising about one-tenth of the total area of the wall is characterized by its uniformly thin smooth wall. It is through this area at a point slightly posterior to its mid-point, that the oviduct opens.

The remaining nine-tenths is not so easily described, since both surfaces are covered by specialized structures. The inner surface is almost entirely covered by rings of scale-like cells 10–30 μ long and 6–15 μ broad at the base (Fig. 10, D, cal.). The scale-like cells occur in regularly circular groups, two to four layers thick (Fig. 10, D_1). When first formed, these cells fold inward at their pointed apices, leaving either a very small opening, or none at all. They become more or less erect, or partially reflexed, much like the calyx of certain flowers. The term calyx describes this structure rather than the entire chamber.

The nature of the tissue beneath these cells is difficult to clearly describe partly because it varies from one to another of the units and partly because it varies greatly as development progresses. In its earliest state these scale-like cells rest on a mass of small irregular cells which form a nearly continuous layer. In the center of this layer, is a small cylindrical pit rounded at its lower end (Fig. 10, D_2). Further development leads to the enlargement


D3
A
sp.gl.d.
sp.
sp.d.
B
B1
D1
ca.
ca.
D2
D4
D
og.
oc.
l.c.
cal.
50 μ

of this pit or to the breakdown, or separation of the small cells, to form a large opening at the base of the scale-like cells. This opening enters the base of an ovariole. The ovariole wall and the ring formed by the base of the outer scales become continuous, and are connected with adjoining ovarioles by a layer of small irregular cells. In each ovariole, the wall is a continuous layer 1.5–2.5 μ thick from the base to near the apex, where it joins with a group of closely massed long cells which gradually narrow until only a single acute tip remains free in the haemolymph. At the base of the ovariole, the wall is usually much wrinkled at this stage, with the membranes separating the component cells indiscernible.

Within the wall, the basal half or more of each ovariole is filled by large cells. In one early callow queen, these large cells occupy about three-quarters of the length of each ovariole. Characteristically, the lowest ones are more or less discoid, unequal in thickness, and multinucleate (Fig. 10, D). Usually these cells do not quite fill the cavity formed by the ovariole wall. Further up in the ovariole, these large cells become irregular so that two to four of them are at the same level (Fig. 10, D_3). In all but some of the lowermost ones, each has a single large spherical to discoid nucleus.

Near or more frequently above the middle of the ovariole, these large cells cease and a mass of small irregular cells is found. The change is always sharp. It is not always possible to see cell

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FIG. 10. Reproductive system of queen.

- A t.s. spermathecal gland showing ductules opening into central lumen; also small and large nuclei
- B Junction spermathecal duct (sp.d.), spermathecal gland duct (sp.gl.d.) and spermatheca (sp.)
- B_1 Wall of spermatheca
- C Outline, upper end of oviduct and small portion of calyx wall (ca.)
- D Ovariole of callow queen, showing calyx-like cells around lower end (cal.), wrinkled ovariole wall at lowest portion; large cells within (l.c.) oöcytes (oc.), oögonia (og.), disk-shaped cells and apical group of elongate cells
- D_1 t.s. ovariole, near base
- D_2 l.s. ovariole at base
- D_3 t.s. ovariole above base showing large cells
- D_4 t.s. zone of disk-shaped cells

membranes, especially in the central part of the mass (Fig. 10, D, oc). These small nucleate cells occur in nearly the entire length of the upper ovariole, being replaced near the apex by a row of uniform discoid cells (Fig. 10, D, left, and D_4). Near the apex, these cease, the long slender cells described above forming the apex of the ovariole (Fig. 10, D, extreme left). These ovarioles almost cover the entire chamber of the ovary except for the smooth area noted above.

The usual development described in all ant species occurs in this upper part of the ovariole. Certain cells increase in size, and become enveloped in a specialized layer of cells, the follicular epithelium, which soon surround the rapidly enlarging oöcyte except for a small region at the upper end. Above each oöcyte, a group of large irregular cells develop, each one containing a large nucleus. These are the trophocytes or nurse cells. This occurs in the upper part of each ovariole of a callow queen while the large cells filling the basal half persist unchanged. Presently, these large cells begin to break down and disappear, this process beginning with the lowermost and progressing upwards until the entire mass of cells has completely disappeared. The now nearly mature oöcytes, some of which are becoming invested with the two membranes characteristic of mature eggs, are slowly moving to the lower part of the ovariole. Before this movement has progressed very far, the lower part of the ovariole wall has become greatly wrinkled.

As the queen passes through late callow and into post-callow condition, certain changes occur in the reproductive organs. Most obvious among these is the increase in size of the chamber of the ovary, which doubles its length. The diameter also increases, but not as much as the length. Concurrently, the length of each of the many ovarioles has increased to about the same degree as has the chamber; this increase of the ovariole is accompanied by a change in the cells of the ovariole, the large cells of the lower half gradually becoming dissolute, the small oögonial cells of the upper half increasing in numbers and gradually pushing downward to fill the lower part of the ovariole. Two other less obvious changes have occurred—the first, a gradual elongation and thinning of the scale-like cells of the calyx-like structure, has been noted earlier: the other is a pronounced irregular wrinkling of the wall of the chamber, a change somewhat obscured by the structures growing from the surface. These four changes are the result of growth with age, and are not cyclic.

During the first two to three days of the nomadic phase, each ovariole is formed principally of a long mass of small oögonial cells. Towards the end of the second or early on the third day, small oöcytes are seen in the lowest part of each ovariole. Ocassionally one, or more, partially absorbed eggs (the partially collapsed and wrinkled egg membranes being noticeable) are seen in the lower end of some of the ovarioles. This occurrence may indicate that the queen is old. From the second through the ninth day of the nomadic phase, no conspicuous change occurs: during this interval, there is a gradual increase in the number of oöcytes in each ovariole, accompanied by the formation of a layer of follicular cells around the lowermost of the oöcytes, and the differentiation of groups of nurse cells, or trophocytes, between successive oöcytes in the lower part of the ovarioles.

No study of further changes were possible since queens collected during this part of the nomadic phase were lacking. In queens fixed at the end of the nomadic phase, nearly all the ovarioles have in the lower end one or more mature eggs, identified by the presence of chorion and vitelline membranes. Also, there is the long series of gradually decreasing oöcytes, the lower ones surrounded by follicular epithelial cells, the upper ones without such. Above these, extending nearly to the apex of the ovariole is the long mass of oögonial cells. The most characteristic feature of these ovarioles is the gradual series of cells, from the small undifferentiated cells at the apex to the mature eggs at the mouth. There is striking uniformity of the ovarioles in six queens, fixed on the second day of this phase.

The interval, including the last two or three days of the nomadic phase and the first five or six days of the statary phase, shows considerable variation in the rate of development of the cells of the ovarioles; especially in callow and post-callow queens. Frequently, it is during this interval that mature eggs begin to accumulate in the lower part of each ovariole. There is still one obvious difference—in many queens, the transition from mature eggs to not more than half-developed oöcytes is conspicuous; in other queens, there is no obvious region of separation, each ovariole has a graduated series of cells from the uniformly small undifferentiated cells at the apex through a gradual series of oöcytes and into a series of maturing eggs. These may be differences between queens that are always observable. In any case, all the queens studied reach the same state at or just after the middle of the statary phase, the ovary then containing a large number of mature eggs. The number in each ovariole varies from five to ten, of uniform size, with a gradually decreasing series in the upper part of each ovariole. It is at about the same time that the first eggs are observed in the chamber of the ovary. No exact timing is possible after this event—eggs become more and more numerous in the chamber, appear in the paired oviducts, move into the median oviduct and finally appear in the vagina. During this period, of several days duration, one may count 200–300 eggs in the ovarian chamber, 50–60 in each of the paired oviducts, 20 or more in the median oviduct, but only four or five in the vagina. These eggs are invariably exactly oriented, the longitudinal axis of the egg paralleling the longitudinal axis of the containing part. Nor do the eggs ever show any evidence of distortion of shape due to crowding. Only at the end of this phase are eggs with distorted shapes found. These have been mentioned earlier as characterizing older queens. During the most active egg deposition, eggs are rarely found in the genital entrance or in the bursa copulatrix.

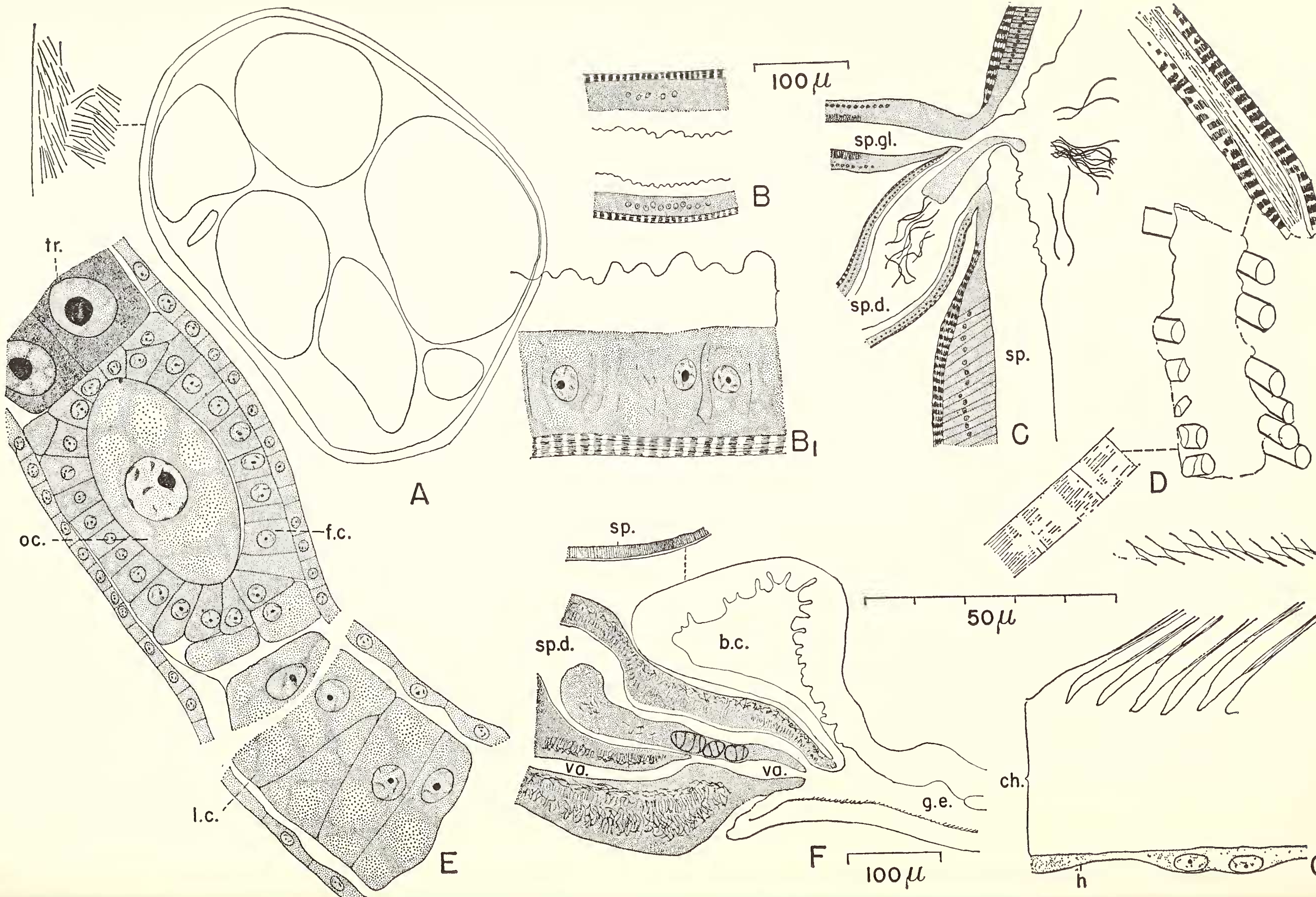
Unfortunately, no *mature* queens taken in the last few days of the statary phase were available for study. The two queens taken nearest the end of this phase were both young individuals, which became the functional queens of new colonies more than a month before capture, subsequent to the division of the parent colonies a few days after their emergence as callows (Schneirla, 1956). The colony of queen '52 H–J, *E. hamatum* completed one nomadic phase following colony division, and was in the fifteenth day of a statary phase when the queen was captured. A large brood of embryos and recently laid eggs were present, and obviously the queen had nearly completed laying her first lot of eggs. The colony of queen '52 B–I_S, *E. burchelli* had also completed one nomadic phase after division, and was in the thirteenth day of the ensuing statary phase when the queen was captured. Embryos and recently laid eggs, estimated at more than 100,000, was found in the colony at the time. The ovaries of these two queens differ considerably, that of *hamatum* having many mature eggs in the chamber, oviducts, and ovarioles, with an abrupt transition from the uppermost egg to a short region of undifferentiated small cells. The ovary of the *burchelli* queen, in contrast, contains not a single egg, and suggests that she had completed her egg deposition. Callows usually are abnormal in their ovarial structures. It seems reasonably that this *burchelli* queen shows the change typifying the end of the statary phase; inasmuch as there is a sudden cessation of egg development, with a row of mature eggs gradually leaving the ovarioles, but no cells developing to replace them.

In prepared sections, the spermatheca is the most conspicuous object in the gaster, especially when filled with sperms, stained dark blue or black by haematoxylin. Eight of the queens studied here are callow, these callow queens have a dense mass of sperms in the spermatheca.

The shapes of the spermathecae varied—two were nearly spherical, the two dimensions of the sagittal sections being 2440 and 2430 μ in the larger, and 1680 and 1660 μ in the smaller one: several were irregularly ovoid, the upper half slightly larger than the lower, or ellipsoid, or even angular. The largest spermatheca measured 3010 μ from top to bottom and was 2020 μ wide; the smallest of these measured 1900 by 1680 μ, larger than the unusually spherical one noted above. Nearly all seemed tilted forward.

The wall of the spermatheca is thick and shows three distinct layers of which the middle one is usually most striking (Fig. 10, B_1). This is formed of tall columnar cells, each containing a single spherical or ellipsoidal nucleus. The nuclei are so regularly located in the cells that they usually form an even layer around the spermatheca; in some individuals, this layer of nuclei is near the base of the cells; often it is in or near the middle of the cells. This layer averages 25–35 μ in thickness; but may vary from 15–50 μ. In nearly all the queens, this layer was uniformly thick; but in few, it was formed of cells varying length, such that the entire layer showed a pattern of uniformly large conical crests evenly spaced on its inner surface. In such cases, the cell at the peak might have a length of 35 μ, those in the thinnest areas measuring only 12 μ.

Within this layer, is a thick intima usually showing a stratified structure, the thin lines separating these strata being vaguely parallel, if one may so describe lines that may be broadly and



A
B
B1
100 μ
C
sp.gl.
sp.d.
sp.
D
E
tr.
oc.
f.c.
l.c.
F
sp.
b.c.
sp.d.
va.
va.
g.e.
100 μ
50 μ
ch.
h
G

often irregularly sinuous. The inner surface of this intima is sharply defined and is usually unevenly and finely sinuous. This intima varies from 40–65 μ in thickness, but is uniform in each individual.

Externally, there is a thin layer of muscle fibres (8–13 μ thick) encircling the spermatheca in a plane parallel to the sagittal section of the gaster. In one large spermatheca, this muscle layer was only 2–3 μ thick, possibly due to the large mass of sperms in the spermatheca.

The spermathecae of the virgin queens, instead of containing sperms are filled with a substance which is uniform throughout the cavity of the spermatheca, and contains many minute granules.

Contents of the spermathecae of the fertile queens are not so easily described due to the conspicuous differences, perhaps indicating the gradual change that occurs during the life of the queen.

Several of the callow queens were found to be fertile.* In each

* Six such queens were available for this study, of which five were captured from the daughter colonies in which they had been established as the single queens for periods between 8 and 31 days after colony division. These were queens '48 H-27_{II}, *E. hamatum,* and '52 B-I_N, '52 B-I_S, '52 B-V, and '55 B-IV_N, *E. burchelli* (Schneirla, 1956). The second, third, and fourth of these queens had delivered their initial batches of eggs before the time of capture.

FIG. 11. Reproductive system fertile queen.

- A Spermatheca with "balls" of sperms; left, part of a sperm "ball," showing surface of embedding substance
- B l.s. long spermathecal duct, near middle
- B_1 Detail, wall of spermathecal duct
- C Detail, spermathecal duct (sp.d.) and a sperm gland (sp.gl.) with part of spermathecal wall (sp.) and sperms in duct and spermatheca
- D Foreign objects found in spermatheca
- E Portion of ovariole, large cells (l.c.) in lower portion, öocyte (oc.) in follicular epithelium (f.c.) and nurse cells (tr.)
- F Detail, union of vagina (va.), spermathecal duct (sp.d.), genital entrance (g.e.) and bursa copulatrix (b.c.)
- G Detail, ventral wall genital entrance, hypodermis (h.) and chitin (ch.) with rows of spines and edge of opposing (upper) wall

Scale: B_1, D, E and G = 50 μ scale; B, C, and F = 100 μ scale.
A = semidiagrammatic

of these queens, spermathecal contents are massed into about eight large ellipsoidal balls (Fig. 11, A). The orientation of the sperms indicates that at the time of fixation these balls were probably in some sort of rotatory motion that caused the sperms to become parallel. Each of these masses is contained in a sharply outlined non-staining substance extending beyond the sperm mass to form an enveloping layer 2–3 μ thick. These sperm masses vary in size, the largest having a length approximately half the diameter of the spermathecal lumen, the smallest measuring less than one quarter of that diameter.

In addition to the sperm balls, are many smaller masses or particles. Some of these are readily identified as small masses of densely aggregated sperms. But others are not so easily identified—among them are smaller masses of muscle tissue in which striations are sharp; other particles seem to be pieces of some coarse spine-like objects, occasionally combined with muscle-tissue or alone; some seem to be small tubes with muscular walls surrounding compact masses of parallel sperms; and some are indeterminate (Fig. 11, D). Possibly, these small objects are from the body of the male even though hasty examination of male abdomens fails to identify them.

In queens, definitely not callow and presumably much older, similar sperm balls are occasionally found in the spermatheca. In these queens, however, there is one striking difference from the callows, that being the presence of a uniformly thin aggregate of sperms throughout the space between the balls. Here also, the balls seen are more irregular in shape, more numerous, and often flattened as if by mutual pressure. Nor were any foreign objects observed here.

In the majority of the queens, the sperms form a single mass

Dr. Schneirla informs me that the sixth of these queens, '48 H-12, *E. hamatum,* was the only one captured before complete division of her parent colony. Since numerous callow *Eciton* queens of this class previously studied by Hagan (1955) and by me have been without sperms, this queen is the first callow discovered to have been fertilized before the completion of colony division. It is Dr. Schneirla's conclusion that this queen, the first of the virgin series to issue from the bivouac of her colony, and removed from her entourage of workers at that time for fixation and preservation (p. 286,—Schneirla and Brown, 1950), had emerged from her cocoon only two or three days earlier, hence must have been fertilized in the bivouac in the intervening period.

that fills the lumen of the spermatheca. In some of the queens, this is a uniformly dense mass of irregularly grouped, entangled sperms. In many of these, are found "pores" penetrating throughout the mass. These "pores" are about 10 μ in diameter. In other queens, the number of sperms per unit of volume becomes progressively less until the number is small and single sperms are widely separated. A decreasing sperm supply in the spermatheca eventually leads to re-insemination of the queen.

The paired spermathecal glands are long, much curved bodies gradually narrowing to a slender rounded apex. Originating on the anterior-dorsal surface of the spermatheca, each of the pair soon turns abruptly, sometimes upward, often laterally, but more frequently downward over the spermathecal surface, eventually ending in the ventral part of the gaster.

The structure of these glands is uniform from base to apex; that of callow queens differs noticeably from that of older queens. In the callow queens, there is on the outer surface a prominent membrane having a single layer of large columnar cells. Each cell contains a single spherical nucleus 8–10 μ in diameter. Membranes separating these cells are clear laterally; they may occasionally clearly show on the upper surface in callow queens, but not in older ones. Within this layer of cells, distinguished by its darker staining, is a lighter staining region containing fine ductules. These ductules narrow gradually from the base, which is 1.5–1.7 μ in diameter, to the apex of about 0.5 μ in diameter. In all ductules, the apex is usually loosely coiled or irregularly curved, and filled with a dark-staining substance. In callow queens, many small ellipsoidal nuclei measuring 1.5–2 by 3–4.5 μ form an irregular layer near the mid-portion of these ductules. No cell membranes were found in this region (Fig. 10, A). In older queens, nuclei were never found in this region. Surrounding the central lumen of the spermathecal glands, is a dark-staining zone about 2 μ thick; passing through this layer, the mouths of the ductules flare widely. The diameters of these spermathecal glands vary from 100–140 μ.

The spermathecal duct in its usual appearance has been well described by Hagan—an unusually long tube, flattened near its union with the vagina, then cylindrical throughout the rest of its length; and having several tight coils. These coils vary greatly, the component rings being sometimes tightly adpressed one to another, sometimes loose, and sometimes absent and replaced by loose irregular loops.

In callow queens, the spermathecal duct differs from that of older queens. In one callow queen, the duct passes downward over the anterior surface of the spermatheca to the level of the median oviduct. Here, the spermathecal duct turns anteriorly and forms a compact irregularly contorted mass. From this mass, the duct passes porteriorly above the median oviduct to end in the dorsal surface of the vagina near its anterior end. In this queen, there is no sign of coiled regions anywhere in the duct. Apparently, continued elongation of the midportion of the duct causes loops to extend anteriorly, and eventually to become pairs of tightly coiled rings of varying length and numbers.

Throughout the greater part of its length, this spermathecal duct is formed of three distinct layers (Fig. 11, B); only in its posterior portion are there four layers, of which two outer layers cannot easily be observed. Surrounding the central lumen, is a thick intima, the inner edge of which is sharply defined. In many individuals, the lumen is greatly reduced by the deep folding of the inner surface of the intima—in extreme cases, nearly obliterating the lumen. At the other extreme, the inner surface of the intima is nearly smooth, and the lumen cylindrical except in the flattened posterior portion. Surrounding the intima, is a single layer of cuboidal cells, each with a single nucleus, 6–8 μ in diameter (Fig. 11, B_1). Membranes bounding these cells are seldom demonstrable, though some dark lines are identifiable as separating membranes. Externally, a third layer is usually in contact with the cellular layer. It is muscular with well-defined striations. These muscle fibres parallel the axis of the duct. In the posterior part of the duct, including the flattened part and varying lengths of the cylindrical portion anterior thereto, a fourth layer composed of muscles, encircles the duct. In these circular muscles, striations are less pronounced than in the longitudinal ones.

The dimensions of the spermathecal duct vary from scarcely 100 μ in diameter to nearly 200 μ. Equally great is the variation of the component layers of the duct, the intima often exceeding the cellular layer; less often, the cellular layer exceeding the intima. The muscle layer is thinner and more uniform than the others, being 4–7 μ thick, except near the posterior end when it thickens.

In three queens, the posterior part of the lumen contains curious elongated plugs of material, usually extending into the lumen of the vagina. These plugs are composed of a darkly staining substance containing a few sperms and several dark, septate ellipsoid conspicuous bodies (Fig. 11, F). Probably these queens were fecundated shortly before being fixed.

In many of the queens studied the entire length of the spermathecal duct is empty. In others, groups of sperms occur irregularly throughout its length. Some of these groups contain 12–24 sperms, others have an estimated several hundred and some groups may contain thousands. Examination shows the sperms are immersed in a non-staining jelly-like substance while in others, the sperms are free of any enveloping substance. When sperms are present in the duct, mature eggs, or very large oöcytes are present in the ovaries. Sperms are often present in the upper end of the spermathecal duct, at least where the duct opens into the lumen of the spermatheca; this is independent of the state of the ovaries.

The union of the spermathecal duct and of the two glands and the way in which these open into the spermathecal lumen varies (Fig. 10, B: Fig. 11, C: Fig. 12, A, B, C). In one variation, the spermathecal duct passes over the anterior surface of the spermatheca to midway in the upper anterior quadrant. As the duct nears this point, the lumen of the duct abruptly enlarges and enters the wall of the spermatheca, where the muscle layer fails to envelop it. Where the duct joins the spermatheca, the two spermathecal glands also join the spermathecal duct, one from each side, so that the lumena of the two glands join the lumen of the duct separately on the dorsal side just before the duct passes into the wall of the spermatheca. In a second, less frequent variation, the spermathecal duct passes dorsally along the anterior wall of the spermatheca. The two glands also extend upwards over the spermathecal wall, but well out towards the lateral surface. Near the level where the duct joins the spermatheca, the glands turn abruptly inward, approaching the duct from opposite sides. The lumina of the duct and the two glands enter the wall of the spermatheca separately, rapidly converge, and join at some point within the spermathecal wall, having a common opening into the lumen of the spermatheca. In a third variation, the duct and the glands join the spermatheca much as in the second case, but the three lumena unite so near the

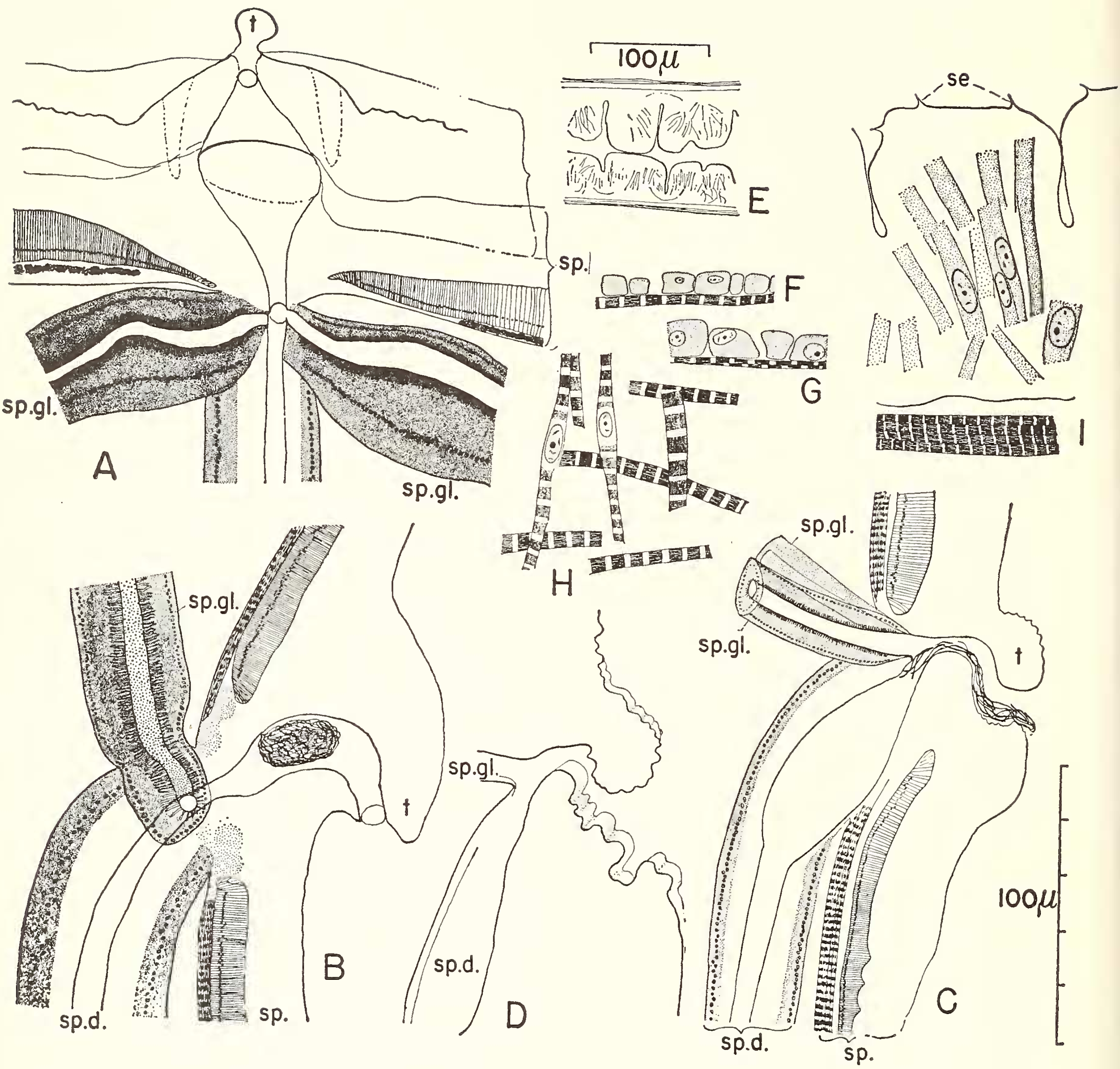


FIG. 12. Reproductive system.

A Part of spermathecal wall (sp.), opening into spermathecal duct, openings of two spermathecal gland ducts (sp.gl.) and "tooth" (t.) Angle of section here exaggerates spermathecal wall thickness

B l.s. spermathecal wall (sp.), spermathecal gland (sp.gl.), and spermathecal duct (sp.d.), with ball of sperms in lumen of duct inner wall of the spermatheca that a wide invagination of the lumen of the spermatheca is formed; and into the inner end of this invagination, the lumena of the glands open separately.

The wall of the spermatheca is thicker around the opening of the spermathecal duct than elsewhere. Usually this thickness produces a low protuberance on the inner wall which may end in a peg-like knob, up to 8 μ in diameter and 15–20 μ long, projecting downward over and below the opening of the duct. This is evident when the opening is directed downward. The opening of the duct may occur through the lower part of the thickened region, and is then directed downward; or it may be through the central region, the opening then facing posteriorly. The actual opening varies from the circular to a broadly elliptical shape. The surface of the wall surrounding the opening may be smooth; often however, showing numerous unequal transverse wrinkles, some forming depressed areas 10 μ deep (Fig. 12, D). In many queens, this region contains many sperms, which stain heavily and thus conceal the nature of this region. Invariably a large mass of sperms collect in or near the opening of the spermathecal duct into the spermatheca. This sperm mass may be continuous with the mass of sperms filling the spermatheca.

In all workers, the reproductive system is of simple structure and unlike that of the queens (Fig. 8, B_1). From the smallest minors to the large soldiers, the structure is similar but differs in size. Occasionally, the system is absent or much reduced.

The reproductive system of the worker normally consists of the genital entrance, vagina, oviduct, an abortive spermathecal body and one or more ovarioles. The genital entrance is a broad shallow space, the walls of which are smooth; posteriorly, it is partially closed by the upturning of the posterior part of the

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C l.s. spermathecal wall (sp.), glands (sp.gl.) and duct (sp.d.), with thin layer of sperms on duct lower wall

D Detail, inner part spermatheca wall and upper lumen of spermathecal duct (sp.d.), and lumen spermathecal gland (sp.gl.) shown at slight angle to emphasize wavy surface of wall

E l.s. median oviduct

F, G Upper (F) and lower (G) end of wall of a paired oviduct of nearly physogastric queen, showing muscle layers

H tg.s., fully inflated (with eggs) oviduct wall, showing muscle layers

I l.s. wall of median oviduct showing spines (se.) and muscles ventral chitin wall. Anteriorly, scarcely any change marks the beginning of the vagina, there being little or no structure that can be called bursa copulatrix. The walls are cellular with small discoid nuclei and no obvious enveloping muscle tissue. In some workers, there is a small featureless structure rising from the upper surface of the vagina ending in a small, solid mass of cells; presumably spermathecal tissue. In other workers, a minute evagination of the dorsal wall of the vagina may be a spermathecal vestige. In many workers, such structures are absent and the dorsal wall of the vagina-oviduct tube is uniformly smooth.

The anterior end of this long slender tube divides to form two short tubes, the paired oviducts, at the end of which the ovarioles are found. In the workers studied the largest number of ovarioles noted was three on each side—six in all. Often, two were found and sometimes (especially in minor workers) only one. When three ovarioles occurred in an ovary, one ovariole was well-developed, the other two small. In ovaries with two ovarioles, the latter were of nearly equal size.

The structure of a worker ovariole is like that of the queens, but greatly reduced. The ovariole wall is a thin layer of squamous cells except at the apex, where a single short lash-like cell occurs. A small group of uniformly small cells is within the wall and as development continues, the cells of the lowermost part of the ovariole become differentiated, showing a large oöcyte surrounded by a layer of small cells, the follicular epithelium (Fig. 8, B, left), and above this a short zone of large nurse cells. In workers studied no ovariole was seen having more than a single developing oöcyte. In three individuals, mature eggs having a well-developed chorion and a thin vitelline membrane were found in the base of the ovarioles. One of these workers was a minor, the other two were majors. These eggs were one-third or less than the corresponding dimensions in eggs of queens.

Very little change in the heart and the digestive system is noted that can be correlated with the alternating contraction and physogastry of the gaster. The heart is slightly elongated during physogastry, and the posterior end may be pulled forward a bit; but any such changes are too small to be convincingly measured. Somewhat more obvious is the elongation of the intestine which at the height of physogastry is tautly stretched in many of the queens; in others, the condition of the intestine lacks tautness.

The change of the peripheal glands in the gaster anterior to the spermatheca has been described earlier; one may recall that during physogastry, the gland cells are displaced to form a single layer, instead of the compact group two to four cells thick.

In the larger elements of the tracheal system, both in the main longitudinal trunk and in the larger branches, the change is obvious. In contracted queens, the walls of these trachea form many closely adpressed unequal folds: during the nomadic phase, these folds gradually spread as much as a two-fold increase in both the length and the diameter of the tracheal tube. This increase may continue into the early days of physogastry; but the mass of enlarging eggs seems to exert enough pressure to cause a decrease in the size of the tracheal elements before full physogastry is reached and a return of the folded condition of the walls.

Fat cells are numerous throughout the thorax and gaster, less abundant in the head. In the gaster, these aggregate in large masses, the fat bodies. Two changes probably occur in these fat cells during a reproductive cycle although they can not be demonstrated in the queens studied. That some queens have larger or more numerous amounts of fatty substance is indicated by the number and nature of the many vacuoles observed in the fat cells. The fatty material may have been removed during preparation of the material for study. The number of vacuoles increase during the nomadic phase, followed by a decrease as that phase ends. This change, however, is one that cannot be properly measured. The change in the nucleus in the fat cell is more easily observed: here again, it is not easy to set any limits for the change observed. In many queens, the nucleus is irregular, with a broad curving outline; in other queens, the nucleus of the fat cell is so collapsed that its outline shows only several irregular thin teeth projecting outward from a narrow body, an appearance usually described as stellate. The plump state of the nucleus is most frequent during the nomadic phase; the stellate, in the statary interval. But the distinction is not absolute—perhaps there are several factors leading to changes in the nucleus, imediately prior to fixation.

One other change is difficult to observe in its entirety. In queens fixed during the nomadic phase, the lumen of the spermathecal duct is empty, with the exception of small masses of sperms frequently found in or near the opening through the spermathecal wall. Earlier in this paper, the presence of a "plug" of material in the mouth of the spermathecal duct of some callow queens was also noted. With these two exceptions, no visible substance is in this duct during the greater part of the nomadic phase. Only near the end of this phase does this condition change. In these final days, masses of sperms appear in the lumen of the spermathecal duct. These masses may be large, containing hundreds or even thousands of sperms, in some sort of unstained substance, the outer surface of which is distinct. Or the sperm masses may be small, containing not more than 100–200. Occasionally, small groups of perhaps a dozen sperms is seen. These groups are observed throughout the length of the lumen: sometimes, few in number and widely separated; sometimes, numerous and close together; seldom is there regularity in their distribution along the lumen. No queen was found with a continuous mass of sperms in the spermathecal duct. The presence of sperms in the duct is easily correlated with mature eggs in the ovarioles or in the tubes through which these eggs pass from the body.

(to be continued)

NOTES ON CONNECTICUT SPHAGNUM BOG

ALEXANDER B. KLOTS
THE CITY COLLEGE OF NEW YORK

RECEIVED FOR PUBLICATION MAY 21, 1962

ABSTRACT

A small Black Spruce bog in northeastern Connecticut is described, and some Lepidoptera from it listed.

Through the kindness of Edwin Way Teale of Hampton, Conn., I was able, in July 1961, to study and collect in a small bog at West Willington, Tolland Co., Connecticut.

No more than about 300 yards long and 50 to 100 yards wide, the bog is bounded on one side by a railroad track and on the other by the fill of a large gravel pit and its lower end is cut by the Wilbur Cross Highway. The construction of the latter probably altered the bog's normal drainage system. The bog is now in a rather late stage, containing no open water or floating mat,